Increasing temperature and decreasing specific leaf area amplify centipede predation impact on Collembola

Mathieu Santonja[a,b,c,*], Adriane Aupic-Samain[d], Estelle Forey[e], Matthieu Chauvat[e]

[a] Univ Rennes, CNRS, ECOBIO UMR 6553, F-35000, Rennes, France
[b] Ecole Polytechnique Fédérale de Lausanne (EPFL), School of Architecture, Civil and Environmental Engineering (ENAC), Laboratory of Ecological Systems (ECOS), Station 2, 1015, Lausanne, Switzerland
[c] Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Site Lausanne, Case Postale 96, 1015, Lausanne, Switzerland
[d] Aix Marseille Univ, Avignon Université, CNRS, IRD, IMBE, Marseille, France
[e] Normandie Univ, UNIROUEN, IRSTEA, ECODIV, FR SCALE CNRS 3730, F-76000, Rouen, France

ABSTRACT

Collembola is an abundant group of soil organisms playing a major role on litter decomposition process and nutrient cycling in forest ecosystems. Habitat structure strongly influences Collembola assemblages as plant litter physical characteristics and quantity provide structural niches and determine the outcome of their interactions with predators. Collembola are also extremely sensitive to environmental conditions such as soil temperature that control their demographic parameters and activity. In this context, increasing temperature with the ongoing climate change can have strong impact on Collembola assemblages and their responses to predation either directly by altering their behaviour or indirectly by altering their habitat structure. We therefore examined how the increase of temperature combined to the decrease of specific leaf area (SLA, a major functional plant trait) of the European common oak (*Quercus robur* L.) and the presence of a centipede predator (Chilopoda: Lithobiidae) will affect the abundance of *Folsomia candida* (Collembola: Isotomidae) in a 5-week microcosm experiment. Increasing temperature, decreasing SLA and presence of centipede altered *F. candida* abundance. We observed a significant temperature × predation interaction suggesting differential effects of increasing temperature on *F. candida* abundance with and without predator. We also observed a significant SLA × predation interaction highlighting that lower SLA decreases *F. candida* abundance only in predator presence. Finally, our findings evidenced that increasing temperature and decreasing SLA amplify the negative effect of centipede predation on *F. candida* abundance, suggesting that both direct and indirect effects of climate change would conjointly strengthen the top-down control of predators on preys.

1. Introduction

Soil biodiversity plays an essential role in ecosystem functioning, especially in biogeochemical cycles [1,2] with feedback on plant growth, ecosystem productivity and overall community structure [3,4]. It has become increasingly clear during the last decades that soil biodiversity and related ecosystem services are extremely threatened by climate change [5,6], through changes in species demographic parameters, species interactions [7,8], and eventually cascading effects on ecosystem processes [9,10]. As predator-prey interactions are a key structuring force in population dynamics [11,12], understanding the effects of climate change on these interactions is of primary importance to predict soil ecosystem responses.

Collembola, among the most widespread and abundant group of soil organisms [13], plays a major role in soil functioning [14] by regulating the microbial (bacterial and fungal) communities, litter decomposition process and nutrient cycling, and consequently feedback on plants [15–18]. Collembola are also strongly top-down controlled by many predators including spiders [18,19], centipedes [20,21] or mites [22,23]. Furthermore, Collembola are often under the influence of habitat structure as plant litter physical characteristics and quantity (i.e. litter thickness) provide niches serving as microhabitats for Collembola [9,19,21,24]. This habitat structure also acts as an important driver of prey-predator interactions by influencing encounter probabilities between Collembola and their predators [19,21].

As Collembola are also extremely sensitive to environmental conditions [13], increasing temperature and decreasing precipitation induced by ongoing climate change [25–27] can have strong direct

impacts on Collembola demographic parameters (e.g. reproduction, development and survival) by altering both soil temperature and moisture conditions [28–30]. As ectothermic organisms, Collembola and their predators generally exhibit greater activity with warming because of elevated metabolic demands [31]. Several experimental field studies, simulating the impact of future climatic conditions in grassland and forest ecosystems, reported a decline in Collembola abundance and diversity in warmer and drier soil conditions, whereas they increased in warmer and wetter soils [9,30,32–34]. While there is a recent wealth of literature on warming effect on prey-predator interactions [26,35–37], few attempts have been made on belowground organisms. For example Thakur et al. [23] reported that predatory mites (*Hypoaspis aculeifer* and *H. miles*) reduced Collembola coexistence (*Folsomia candida* and *Proisotoma minuta*) with increasing temperature.

In addition, the ongoing climate change can also indirectly affect Collembola by altering litter physical characteristics and quantity produced by plants with thus cascading effects on both the food resource and microhabitat availability for Collembola as well as the outcome of their interactions with predators. In fact, climatic conditions strongly control leaf traits and consequently induce changes in litter traits [38–40]. Plants under warmer and drier climates tend to have thicker leaves (i.e. sclerophylly) and lower specific leaf area (SLA) in order to reduce water loss [40,41]. For example, Graça and Poquet [42] reported that SLA of *Quercus robur* and *Alnus glutinosa* leaves decreased with increasing temperature across a wide European climatic gradient. As a consequence, for hemi- and epedaphic Collembola (i.e. living on the soil surface and in the leaf litter), this decrease in SLA could imply (i) a lower surface area for fungal colonization leading to a reduced fungal grazing, as well as (ii) less spatial refuges and higher probability to encounter their predators. However, to our knowledge, no previous study attempted to evaluate the consequences of a decrease in SLA on Collembola populations and their interactions with predators.

Thus, our current understanding of soil organisms' responses to climate change drivers is still limited by a lack of studies addressing conjointly both direct and indirect effects of climate change on these organisms and their interactions. To address this gap, we designed a full factorial experiment in order to evaluate how the increase of atmospheric temperature (15 °C, 20 °C and 25 °C), the decrease of SLA (15.9 ± 0.5 *vs.* $11.7 \pm 0.3 \, mm^2 \, mg^{-1}$) of European oak leaves (*Quercus robur* L.) and the presence or absence of a centipede predator (Chilopoda: Lithobiidae) affect the abundance of *Folsomia candida* (Collembola: Isotomidae) in a 5-week microcosm experiment. The elevated temperature treatments were established in order to represent moderate (+5 °C) to high (+10 °C) climate warming scenarios [27], whereas the lowest temperature treatment was based on the climate at which *F. candida* was thermally acclimated (i.e. 15 °C). The decrease of SLA was established to simulate the impact of lower surface area for a same litter mass leading to an alteration of habitat structure. Previous to the experimentation, we carefully checked that the two oak litters (high and low SLA) only differed in their physical traits and not on their chemical traits (i.e. C:N ratio and phenolic concentration). We hypothesized that increasing temperature would induce higher predation effects on *F. candida*, as both prey and predator become more active and must encounter each other more frequently. We also hypothesized that decreased SLA would induce higher predation effects on *F. candida*, as a decrease in habitat complexity provides less spatial refuges for the prey population. Finally, the combination of both direct (i.e. temperature) and indirect (i.e. habitat structure) effects of climate change would conjointly strengthen the top-down control of predator on *F. candida*.

2. Materials and methods

2.1. Material collection

2.1.1. Leaf litter

The experiment was conducted using leaf litter of a common and widespread deciduous tree in temperate European forest: the European oak (*Quercus robur* L.). Freshly-abscised shade leaves were collected on 5 individuals during the litter fall period (autumn 2016) in the Paimpont Forest (48°01′N, 2°10′W) and in the Rennes Forest (48°11′N, 1°34′W), northwestern France. In February 2017, 200 g of the leaf litter from both forests were enclosed in 0.5-mm mesh size litterbags and put on the litter layer under oak trees of the University of Rennes 1 campus (48°07′N, 1°38′W) in order to allow litter microbial colonization. Litter samples were collected after 2 months, dried at 40 °C for 48 h and frozen at −18 °C for 48 h in order to remove animals, and then stored in a dark room at ambient temperature until the start of the experiment.

Ten leaves were used to determine the specific leaf area (SLA) of *Q. robur* leaves for each forest. SLA was calculated as the ratio between leaf area and leaf dry weight and determined by weighing (± 0.01 mg) 3 leaf disks obtained with a cork borer (10 mm diameter) from the 10 randomly chosen leaves [42]. The leaf dry weight was determined after drying leaf samples at 60 °C for 48 h. Oak leaves of Paimpont Forest showed a mean SLA of $15.9 \pm 0.5 \, mm^2 \, mg^{-1}$ (thereafter high SLA) while those of Rennes Forest showed a significant 26% lower SLA with a mean of $11.7 \pm 0.3 \, mm^2 \, mg^{-1}$ (thereafter low SLA) (t-test = 7.0, $P < 0.001$). In addition to SLA, C:N ratio and phenolic concentration of the two litter types were measured as these two plant functional traits were reported to also influence Collembola population dynamics [9,24,43]. Carbon and N concentrations were determined by thermal combustion using a CN analyzer. Phenolic concentration was measured colorimetrically using the method described in Santonja et al. [44] with gallic acid as a standard. Leaf litter types of high and low SLA showed no significant difference in both C:N ratio (37.6 ± 0.6 *vs.* 40.6 ± 1.1, respectively; t-test = −2.3, $P = 0.063$) and phenolic concentration (49.3 ± 0.8 *vs.* $51.8 \pm 0.9 \, mg \, g^{-1}$, respectively; t-test = −1.8, $P = 0.123$). As our research hypothesis was based on a physical effect of *Quercus* litter on predator-prey interaction (i.e. habitat structure) and not on a chemical effect of this litter (i.e. trophic or toxic role), we considered that we used two litter types exhibiting similar chemical properties but distinct physical properties to perform our experiment.

2.1.2. Collembola and centipede

The experiment was conducted using two well-represented invertebrate groups from the leaf litter of European oak (*Quercus robur* L.) forests: Collembola as the prey and Chilopoda as the predator. Collembola used in this experiment was *Folsomia candida* (Collembola: Isotomidae), a parthenogenetic and ubiquitous hemiedaphic species known as fungivorous and frequently used in laboratory experiment [23,45]. Individuals were reared in plastic boxes (5.5 cm diameter × 7 cm height) containing a flat mixture of plaster of Paris and activated charcoal in a ratio 9:1, permanently water saturated. Individuals had been cultured at 15 °C and fed *ad libitum* with dry yeast pellets. To synchronize the age of the organisms, oviposition was stimulated by placing adults on a new breeding substrate [45]. After oviposition, adults were removed and the eggs hatched 3–4 days later. To ensure that the population was as homogeneous as possible, eggs were placed in a large container and juveniles were fed for the first time altogether. We used 10–12 days juveniles of similar size (0.90 ± 0.08 mm; n = 10) that were starved 48 h before the start of the experiment.

Lithobiid centipedes (Chilopoda: Lithobiidae) were used as predator in this experiment. They are known as active predators that live in the upper soil layers pursuing prey such as Collembola [13,46]. The centipedes were manually collected by sifting oak leaf litter of the Paimpont Forest. After collection, collected centipede individuals of similar size (10.81 ± 0.65 mm; n = 10) were kept separate from each other in moistened plastic boxes at 15 °C and were fed *ad libitum* with *F. candida* individuals. Centipede individuals were also starved 48 h before the start of the experiment.

2.2. Experimental setup

We tested the effects of three temperatures (15 °C, 20 °C, and 25 °C), two SLA (low *vs.* high) and centipede predation (no predator *vs.* predator presence) on Collembola abundance in a full factorial experiment. Each combination was replicated 7 times and then led to the construction of 84 microcosms, i.e. 3 temperatures × 2 SLA × 2 predation levels × 7 replicates. Plastic boxes (12 cm diameter × 10 cm height covered by a nylon net to allow air circulation) were used as microcosms. Each microcosm was filled with 2 g (dry mass) oak leaf litter. In order to keep the base of microcosm moist, litter was added on top of a double layer of filter paper. In order to make the litter adequately moist and to stimulate microbial growth, 50 mg of yeast in 5 mL of deionized water were added on top of the litter 4 days before animals were added. Thirty individuals of *F. candida* were added into each of 84 microcosms at the start of the experiment. In order to allow prey acclimation to leaf litter habitat, one centipede individual was added 2 days after *F. candida* in each treatment including a predator (i.e. 42 microcosms).

The experiment was performed during 5 weeks in climate-controlled rooms (Percival AR-41L3) with a 12 h: 12 h light: dark photoperiod, a constant temperature (15 °C, 20 °C or 25 °C), and a constant 80% air humidity as centipedes are very sensitive to desiccation [47,48]. The microcosms were kept moist by adding 1 ml of deionized water every 2 days. The 15 °C treatment corresponded to the Collembola culture temperature, the 20 °C and 25 °C treatments to a +5 °C and +10 °C increase, respectively. The two SLA levels (15.9 ± 0.5 *vs.* 11.7 ± 0.3 mm² mg⁻¹) were used in order to simulate the impact of a reduction in leaf surface area (i.e. 31800 *vs.* 23400 mm² for 2 g of oak leaf litter) on Collembola fitness and Collembola-centipede interaction. At the end of the experiment, centipedes were removed by hand and leaf litter of each microcosm was placed on a Berlese-Tullgren funnel to collect Collembola. Individuals were harvested in 90% ethanol and then counted under a stereomicroscope.

2.3. Statistical analyses

Statistical analyses were performed using R software (version 3.4.2). A generalized linear model (GLM), followed by post-hoc multiple comparisons (Tukey contrasts), was used to test for the effects of temperature, SLA, centipede predation, and their interactions on Collembola abundance. We fitted the GLM model specifying a Poisson error distribution and log link function because the response variable was count data (i.e. number of Collembola per microcosm).

3. Results

Temperature, SLA and predation treatments had significant effects on Collembola abundance (Table 1, Fig. 1). On the whole experiment, we found that Collembola abundance was the highest at 20 °C and the lowest at 25 °C (Fig. 1a). For SLA, Collembola abundance was higher

Table 1
Output of the general linear model testing for the effects of temperature (15 °C, 20 °C and 25 °C), SLA (low *vs.* high), predation (no predator *vs.* predator presence), and their interactions on Collembola abundance. d.f. = degrees of freedom. Chi-squared (χ^2) and associated *P*-values (with the respective symbols * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$) are indicated.

	d.f.	χ^2	*P*-value
Temperature (T)	2	121.3	***
SLA (S)	1	7.4	**
Predation (P)	1	22.2	***
T × S	2	0.1	
T × P	2	57.3	***
S × P	1	12.4	***
T × S × P	2	8.9	*

with high SLA than with low SLA (Fig. 1b). Lastly, predation treatment also altered Collembola abundance with higher Collembola abundance in absence of predator (Fig. 1c). However, significant interactions between temperature and predation treatments, between SLA and predation treatments, and between the three treatments were observed (Table 1).

The interaction between temperature and predation treatments suggested that increasing temperature differentially affected Collembola abundance with or without a predator (Table 1, Fig. 2). Without predator, +5 °C favored Collembola abundance (+27% compared to 15 °C) whereas +10 °C negatively affected Collembola abundance (−18% compared to 15 °C). In presence of a predator, there was no difference in Collembola abundance between 15 °C and 20 °C, while Collembola abundance strongly decreased at 25 °C (−55% compared to 15 °C). Furthermore, the negative effect of predation increased with increasing temperature, as the density of *F. candida* was reduced by 26%, 34%, and 59% at 15 °C, 20 °C and 25 °C, respectively.

The interaction between SLA and predation treatments suggested that the decrease of SLA negatively affected Collembola abundance only in predator presence (Table 1, Fig. 3). Furthermore, the negative effect of predation increased with the decrease of SLA, from a 28% reduction of Collembola abundance at high SLA to a 50% reduction at low SLA.

The interaction between temperature, SLA and predation treatments suggested that the combinations of specific temperature and SLA treatments conjointly alter the predator control of Collembola abundance (Table 1). In fact, the greatest top-down control was observed at 20 °C on low SLA (i.e. 70% reduction of Collembola abundance, Table 2), while the lowest top-down control was observed at 15 °C on high SLA (i.e. 18% reduction of Collembola abundance, Table 2).
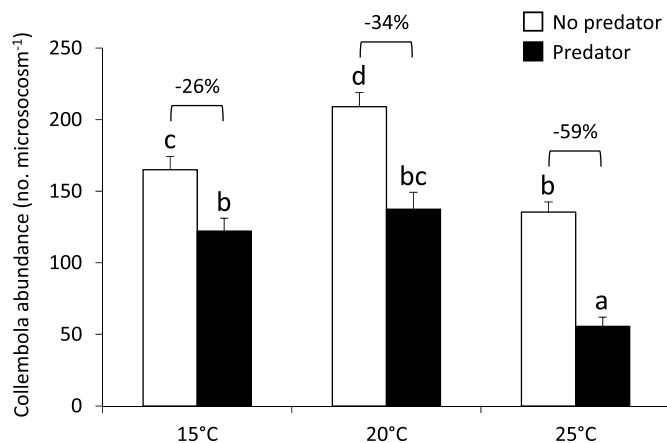
4. Discussion

As expected, Collembola abundance was depressed by the presence of a centipede. This result is in accordance with previous studies, which reported that centipedes have strong negative effects on Collembola abundance [21,49,50]. In agreement with our first hypothesis, we demonstrated that predation effects became stronger with increasing temperature, from −26% at 15 °C to −59% at 25 °C. Grgic and Kos [51] reported optimal temperatures for some European Lithobiidae species between 12 °C and 22 °C, while Chitty [52] reported this temperature range for temperate centipede species between 20 °C and 25 °C, suggesting that the centipedes during our experiment were active foragers. As ectothermic organisms, by increasing their activities with increasing temperature because of elevated metabolic demands [31], higher encounter probabilities between Collembola and centipede induced this short-term increase of predation effects. Our result supports the recent findings of Thakur et al. [10] that also highlighted higher predation effects upon Collembola with increasing temperature. Interestingly, we also found an increase in Collembola abundance with +5 °C increase in temperature that could compensate for the predation impact, as we did not observe a difference in Collembola abundances between the treatments at 15 °C and 20 °C in centipede presence (Fig. 2). Our observation of a maximum abundance of *F. candida* at 20 °C is consistent with the general sigmoid curve obtained when considering the response of an organism over the whole temperature range where development may occur [53]. Stam et al. [54] reported a decrease in clutch size (number of eggs) of *F. candida* at temperature exceeding 22 °C compared with temperature around 15 °C. Fountain and Hopkin [45] also reported an optimal temperature for hatching success at 21 °C for *F. candida*. However, Collembola abundance was strongly reduced with +10 °C, and this direct negative effect, coupled with centipede presence, induced a strong decline of *F. candida* population.
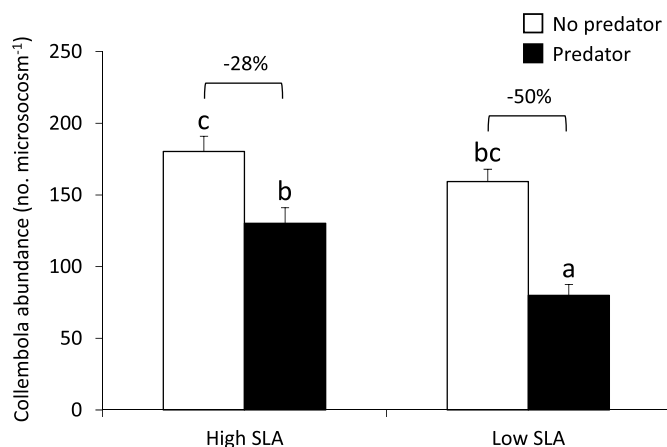
In agreement with our second hypothesis, we also demonstrated that decreasing specific leaf area (SLA) induced higher predation effects on a Collembola population. In line with our findings, two previous
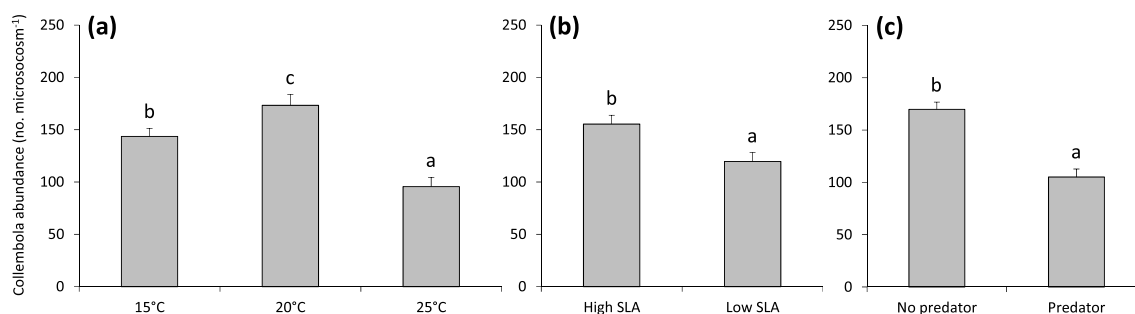
Fig. 1. Effects of (a) temperature, (b) SLA and (c) predation treatments on Collembola abundance. Each bar represents the mean value $\pm$ SE; n = 28 in (a) and n = 42 in (b) and (c). Different letters denote significant differences among treatments with a < b < c.

Fig. 2. Collembola abundance according to the Temperature × Predation interaction. Each bar represents the mean value $\pm$ SE; n = 14. Different letters denote significant differences among treatments with a < b < c < d.

Fig. 3. Collembola abundance according to the SLA × Predation interaction. Each bar represents the mean value $\pm$ SE; n = 21. Different letters denote significant differences among treatments with a < b < c.

Table 2
Collembola abundance (mean $\pm$ SE; n = 7) according to temperature (15 °C, 20 °C and 25 °C), SLA (low *vs.* high), and centipede predation (no predator *vs.* predator presence) treatments.

Temperature	SLA	No predator		Predator	
15 °C	High	174.4	± 13.9	142.7	± 11.5
15 °C	Low	155.7	± 12.1	101.6	± 8.9
20 °C	High	222.7	± 16.2	175.0	± 9.0
20 °C	Low	195.3	± 10.8	100.0	± 7.1
25 °C	High	144.0	± 10.9	73.0	± 7.4
25 °C	Low	126.9	± 8.7	38.1	± 7.3

(*Fagus sylvatica*), highlighting the importance of habitat size in the encounter probability between a predator and its prey. Kalinkat et al. [21] demonstrated thus that increasing litter quantity reduced the encounter rates by diluting the prey population to lower density. In the present study, in addition to the importance of i) litter presence [19] and ii) litter quantity [21], we demonstrated for the first time the key importance of a leaf morphological trait as a regulating factor of predator-prey interactions in a leaf litter system. In consequence, the litter habitat modifications mediated by decreasing both litter quantity production [55] and leaf litter SLA [42] in response to climate change would conjointly amplify the predatory control of Collembola populations by decreasing refuge availability and increasing the encounter rate with their predators.

Finally, we also confirmed our last expectation that both increasing temperature and decreasing SLA conjointly strengthen the top-down control of a centipede predator on a *F. candida* population. In fact, the highest top-down effect was observed at the highest temperature coupled with the lowest SLA. A strong decrease of Collembola abundance could, in turn, leads to a negative impact on their predator population with profound repercussions on soil food web structure. Additionally, these soil cascading trophic effects might have consequences for feedback on plants, as the presence and identity of Collembola can influence nutrient availability for plants, plant traits and strategy, with consequences on both plant productivity and reproduction [9,16–18]. As species interactions provide the mechanistic link between warming and ecosystem functions [11,56], our study suggests that predicting the consequences of climate change may be far from trivial and needs to take into account both direct and indirect effects of climate change to better understand the outcome of short-term dynamics of predator-prey interactions.

Acknowledgement

short-term experiments at low temperatures revealed the importance of habitat structure for the per capita interaction strengths of generalist predators on their Collembola prey [19,21]. In a 24 h experiment at 18 °C day: 16 °C night regime, Vucic-Pestic et al. [19] showed a decrease in consumption rate by a spider (*Pardosa lugubris)* on its Collembola prey (*Heteromurus nitidus*) in presence of moss (*Polytrichum formosum*), highlighting the importance of refuge presence for the prey. In a 24 h experiment at 15 °C, Kalinkat et al. [21] reported a decrease in consumption rate of a predator centipede (*Lithobius mutabilis*) on its Collembola prey (*H. nitidus*) according to the increase of litter quantity

for providing experimental infrastructures.

References

[1] R. Bardgett, The Biology of Soil: a Community and Ecosystem Approach, Oxford University Press, Oxford, 2005.

[2] S. Hättenschwiler, A.V. Tiunov, S. Scheu, Biodiversity and litter decomposition in terrestrial ecosystems, Annu. Rev. Ecol. Evol. Syst. 36 (2005) 191–218, https://doi.org/10.1146/annurev.ecolsys.36.112904.151932.

[3] D.A. Wardle, K.I. Bonner, G.M. Barker, Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores, Funct. Ecol. 16 (2002) 585–595, https://doi.org/10.1046/j.1365-2435.2002.00659.x.

[4] J.M. Gobat, M. Aragno, W. Matthey, Le sol vivant: bases de pédologie, biologie des sols, Presse Polytechniques et Universitaires Romandes, Lausanne, 2010.

[5] J.C. Blankinship, P.A. Niklaus, B.A. Hungate, A meta-analysis of responses of soil biota to global change, Oecologia 165 (2011) 553–565, https://doi.org/10.1007/s00442-011-1909-0.

[6] J.M. Montoya, D. Raffaelli, Climate change, biotic interactions and ecosystem services, Philos. Trans. R. Soc. Lond. B Biol. Sci. 365 (2010) 2013–2018, https://doi.org/10.1098/rstb.2010.0114.

[7] J.M. Tylianakis, R.K. Didham, J. Bascompte, D.A. Wardle, Global change and species interactions in terrestrial ecosystems, Ecol. Lett. 11 (2008) 1351–1363, https://doi.org/10.1111/j.1461-0248.2008.01250.x.

[8] W.H. van der Putten, M. Macel, M.E. Visser, Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels, Philos. Trans. R. Soc. Lond. B Biol. Sci. 365 (2010) 2025–2034, https://doi.org/10.1098/rstb.2010.0037.

[9] M. Santonja, C. Fernandez, M. Proffit, C. Gers, T. Gauquelin, I.M. Reiter, W. Cramer, V. Baldy, Plant litter mixture partly mitigates the negative effects of extended drought on soil biota and litter decomposition in a Mediterranean oak forest, J. Ecol. 105 (2017) 801–815, https://doi.org/10.1111/1365-2745.12711.

[10] M.P. Thakur, P.B. Reich, S.E. Hobbie, A. Stefanski, R. Rich, K.E. Rice, ... N. Eisenhauer, Reduced feeding activity of soil detritivores under warmer and drier conditions, Nat. Clim. Change 8 (2018) 75, https://doi.org/10.1038/s41558-017-0032-6.

[11] A.N. Laws, Climate change effects on predator-prey interactions, Curr. Opin. Insect Sci. 23 (2017) 28–34, https://doi.org/10.1016/j.cois.2017.06.010.

[12] O.J. Schmitz, Behaviour of predators and prey and links with population-level processes, in: P. Barbarosa, I. Castellanos (Eds.), Ecology of Predator-prey Interactions, Oxford University Press, New York, 2005, pp. 256–278.

[13] S.P. Hopkin, Biology of Springtails (Insecta: Collembola), Oxford University Press, Oxford, 1997.

[14] J. Rusek, Biodiversity of Collembola and their functional role in the ecosystem, Biodivers. Conserv. 7 (1998) 1207–1219.

[15] R.G. Cragg, R.D. Bardgett, How changes in soil faunal diversity and composition within a trophic group influence decomposition processes, Soil Biol. Biochem. 33 (2001) 2073–2081, https://doi.org/10.1016/S0038-0717(01)00138-9.

[16] J. Filser, The role of Collembola in carbon and nitrogen cycling in soil, Pedobiologia 46 (2002) 234–245, https://doi.org/10.1016/S0031-4056(04)70139-0.

[17] E. Forey, S.F. Coulibaly, M. Chauvat, Flowering phenology of a herbaceous species (Poa annua) is regulated by soil Collembola, Soil Biol. Biochem. 90 (2015) 30–33, https://doi.org/10.1016/j.soilbio.2015.07.024.

[18] K.L. Lawrence, D.H. Wise, Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition, Pedobiologia 44 (2000) 33–39, https://doi.org/10.1078/S0031-4056(04)70026-8.

[19] O. Vucic-Pestic, K. Birkhofer, B.C. Rall, S. Scheu, U. Brose, Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction, Pedobiologia 53 (2010) 307–312, https://doi.org/10.1016/j.pedobi.2010.02.003.

[20] B. Günther, B.C. Rall, O. Ferlian, S. Scheu, B. Eitzinger, Variations in prey consumption of centipede predators in forest soils as indicated by molecular gut content analysis, Oikos 123 (2014) 1192–1198, https://doi.org/10.1111/j.1600-0706.2013.00868.x.

[21] G. Kalinkat, U. Brose, B.C. Rall, Habitat structure alters top-down control in litter communities, Oecologia 172 (2013) 877–887, https://doi.org/10.1007/s00442-012-2530-6.

[22] M.P. Thakur, N. Eisenhauer, Plant community composition determines the strength of top-down control in a soil food web motif, Sci. Rep. 5 (2015) 9134, https://doi.org/10.1038/srep09134.

[23] M.P. Thakur, T. Künne, J.N. Griffin, N. Eisenhauer, Warming magnifies predation and reduces prey coexistence in a model litter arthropod system, Proc. R. Soc. B. 284 (2017) 20162570, https://doi.org/10.1098/rspb.2016.2570.

[24] M. Sauvadet, M. Chauvat, N. Fanin, S. Coulibaly, I. Bertrand, Comparing the effects of litter quantity and quality on soil biota structure and functioning: application to a cultivated soil in Northern France, Appl. Soil Ecol. 107 (2016) 261–271.

[25] C. Bellard, C. Bertelsmeier, P. Leadley, W. Thuiller, F. Courchamp, Impacts of climate change on the future of biodiversity, Ecol. Lett. 15 (2012) 365–377, https://doi.org/10.1111/j.1461-0248.2011.01736.x.

[26] S.E. Gilman, M.C. Urban, J. Tewksbury, G.W. Gilchrist, R.D. Holt, A framework for community interactions under climate change, Trends Ecol. Evol. 25 (2010) 325–331, https://doi.org/10.1016/j.tree.2010.03.002.

[27] IPCC, Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK and New York, NY, USA, 2014.

[28] P. Kardol, W.N. Reynolds, R.J. Norby, A.T. Classen, Climate change effects on soil microarthropod abundance and community structure, Appl. Soil Ecol. 47 (2011) 37–44, https://doi.org/10.1016/j.apsoil.2010.11.001.

[29] Z. Lindo, Warming favours small-bodied organisms through enhanced reproduction and compositional shifts in belowground systems, Soil Biol. Biochem. 91 (2015) 271–278, https://doi.org/10.1016/j.soilbio.2015.09.003.

[30] G.L. Xu, T.M. Kuster, M.S. Günthardt-Goerg, M. Dobbertin, M.H. Li, Seasonal exposure to drought and air warming affects soil Collembola and mites, PLoS One 7 (2012) e43102, , https://doi.org/10.1371/journal.pone.0043102.

[31] J.F. Gillooly, J.H. Brown, G.B. West, V.M. Savage, E.L. Charnov, Effects of size and temperature on metabolic rate, Science 293 (2001) 2248–2251, https://doi.org/10.1126/science.1061967.

[32] J. Harte, A. Rawa, V, Price Effects of manipulated soil microclimate on mesofaunal biomass and diversity, Soil Biol. Biochem. 28 (1996) 313–322, https://doi.org/10.1016/0038-0717(95)00139-5.

[33] N. Lindberg, J.B. Bengtsson, T. Persson, Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand, J. Appl. Ecol. 39 (2002) 924–936, https://doi.org/10.1046/j.1365-2664.2002.00769.x.

[34] A. Pflug, V. Wolters, Influence of drought and litter age on Collembola communities, Eur. J. Soil Biol. 37 (2001) 305–308, https://doi.org/10.1016/S1164-5563(01)01101-3.

[35] K.C. Abbott, J.P. Harmon, N.S. Fabina, The challenge of predicting temperature effects on short-term predator-prey dynamics, Popul. Ecol. 56 (2014) 375–392, https://doi.org/10.1007/s10144-013-0426-x.

[36] P. Amarasekare, Effects of temperature on consumer-resource interactions, J. Anim. Ecol. 84 (2014) 665–679, https://doi.org/10.1111/1365-2656.12320.

[37] B.C. Rall, O. Vucic-Pestic, R.B. Ehnes, M.C. Emmerson, U. Brose, Temperature, predator-prey interaction strength and population stability, Global Change Biol. 16 (2010) 2145–2157, https://doi.org/10.1111/j.1365-2486.2009.02124.x.

[38] Y. Chen, W. Han, L. Tang, Z. Tang, J. Fang, Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form, Ecography 36 (2011) 178–184, https://doi.org/10.1111/j.1600-0587.2011.06833.x.

[39] P.B. Reich, J. Oleksyn, Global patterns of plant leaf N and P in relation to temperature and latitude, Proc. Natl. Acad. Sci. U.S.A. 101 (2004) 11001–11006, https://doi.org/10.1073/pnas.0403588101.

[40] I.J. Wright, P.B. Reich, J.H.C. Cornelissen, D.S. Falster, P.K. Groom, K. Hikosaka, ... M. Westoby, Modulation of leaf economic traits and trait relationships by climate, Global Ecol. Biogeogr. 14 (2005) 411–421, https://doi.org/10.1111/j.1466-822x.2005.00172.x.

[41] S.E. Pallardy, Physiology of Woody Plants, Academic Press, Amsterdam, 2008.

[42] M.A.S. Graça, J.M. Poquet, Do climate and soil influence phenotypic variability in leaf litter, microbial decomposition and shredder consumption? Oecologia 174 (2014) 1021–1032, https://doi.org/10.1007/s00442-013-2825-2.

[43] M. Chomel, C. Fernandez, A. Bousquet-Mélou, C. Gers, Y. Monnier, M. Santonja, T. Gauquelin, R. Gros, C. Lecareux, V. Baldy, Secondary metabolites of Pinus halepensis alter decomposer organisms and litter decomposition during afforestation of abandoned agricultural zones, J. Ecol. 102 (2014) 411–424, https://doi.org/10.1111/1365-2745.12205.

[44] M. Santonja, V. Baldy, C. Fernandez, J. Balesdent, T. Gauquelin, Potential shift in plant communities with climate change in a Mediterranean Oak forest: consequence on nutrients and secondary metabolites release during litter decomposition, Ecosystems 18 (2015) 1253–1268, https://doi.org/10.1007/s10021-015-9896-3.

[45] M.T. Fountain, S.P. Hopkin, Folsomia Candida (Collembola): a "standard" soil arthropod, Annu. Rev. Entomol. 50 (2005) 201–222, https://doi.org/10.1146/annurev.ento.50.071803.130331.

[46] D.C. Coleman, J.D.A. Crossley, P.F. Hendrix, Fundamentals of Soil Ecology, Elsevier Academic Press, San Diego, CA, USA, 2004.

[47] M. Jabin, Influence of Environmental Factors on the Distribution Pattern of Centipedes (Chilopoda) and Other Soil Arthropods in Temperate Deciduous Forests, Cuvillier Verlag, Göttingen, 2008.

[48] J.G.E. Lewis, The Biology of Centipedes, Cambridge University Press, Cambridge, 2006.

[49] O. Ferlian, S. Scheu, M.M. Pollierer, Trophic interactions in centipedes (Chilopoda, Myriapoda) as indicated by fatty acid patterns: variations with life stage, forest age and season, Soil Biol. Biochem. 52 (2012) 33–42, https://doi.org/10.1016/j.soilbio.2012.04.018.

[50] S. Salmon, J.J. Geoffroy, J.F. Ponge, Earthworms and collembola relationships: effects of predatory centipedes and humus forms, Soil Biol. Biochem. 37 (2005) 487–495, https://doi.org/10.1016/j.soilbio.2004.08.011.

[51] T. Grgic, I. Kos, Temperature preference in some centipede species of the genus Lithobius Leach, 1814 (Chilopoda: Lithobiidae), Acta Biol. Slov. 44 (2002) 3–12.

[52] J.R. Chitty, Myriapods (centipedes and millipedes), in: G.A. Lewbart (Ed.), Invertebrate Medicine, Blackwell Publishing, Ames, 2006, pp. 195–203.

[53] T.L. Wagner, H.I. Wu, P.J. Sharpe, R.M. Schoolfield, R.N. Coulson, Modeling insect development rates: a literature review and application of a biophysical model, Ann. Entomol. Soc. Am. 77 (1984) 208–220, https://doi.org/10.1093/aesa/77.2.208.

[54] E.M. Stam, M.A. Van de Leemkule, G. Ernsting, Trade-offs in the life history and energy budget of the parthenogenetic collembolan Folsomia candida (Willem), Oecologia 107 (1996) 283–292, https://doi.org/10.1007/BF00328444.

[55] N. Rodriguez-Ramirez, M. Santonja, V. Baldy, C. Ballini, N. Montès, Shrub species richness decreases negative impacts of drought in a Mediterranean ecosystem, J. Veg. Sci. 28 (2017) 985–996, https://doi.org/10.1111/jvs.12558.

[56] L. Hughes, Biological consequences of global warming: is the signal already apparent? Trends Ecol. Evol. 15 (2000) 56–61, https://doi.org/10.1016/S0169-5347(99)01764-4.